

A NEW SPECIES OF *BIVIBRANCHIA*  
(PISCES: CHARACIFORMES) FROM  
SURINAM, WITH COMMENTS  
ON THE GENUS

Richard P. Vari

*Abstract.*—The genus *Atomaster*, described by Eigenmann and Myers (1927) for a single contained species, *A. velox*, is placed as a synonym of *Bivibranchia* Eigenmann. *Bivibranchia* is characterized by unique elaborations of the portions of the glossopharyngeal and vagus nerves innervating the branchial basket, and of the vagal lobe of the medulla oblongata. Derived modifications of the dorsal portions of the third and fourth pleural ribs, the associated parapophyses and articular fossae, and the intercostal ligaments of the first four ribs distinguish *Bivibranchia* within the Hemiodontidae. These characters and a variety of unique alterations of the jaws, suspensorium, and gill arches unite the three species of *Bivibranchia* (sensu lato) as a monophyletic lineage within the Hemiodontidae.

*Bivibranchia bimaculata*, an inhabitant of black acidic waters, is described as new from the Corantijn River drainage system of western Surinam. The species is distinguished from *B. protractila* and *B. velox*, the other species in the genus, by the two distinct dark, midlateral spots on the body, one above the pelvic fins and one on the caudal peduncle. Meristic and morphometric differences further distinguish *B. bimaculata* from its congeners.

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One of the most unusual taxa of New World characiforms is the genus *Bivibranchia* proposed by Eigenmann (1912:258) for the single contained species, *B. protractila*, described in the same publication (1912:259) based on specimens from the Essequibo River system of Guyana. That highly modified genus differed from all characiforms known at that time in its markedly protractile upper jaw, fleshy dendritic gill rakers, and a distinctive valvular apparatus on the roof of the mouth (see Eigenmann 1912:pl. 33, figs. 1-5). Subsequently Eigenmann and Myers (1927:565) proposed a new genus and species, *Atomaster velox*, for a second species of protractile-mouth characiform collected in the Rio Tocantins of Brazil. As noted by those authors, the two genera were very similar other than for the small ctenoid scales of *Atomaster* which contrasted with the larger cycloid scales of *Bivibranchia*. Roberts (1974:432), although lacking specimens of *Atomaster* for comparison with *Bivibranchia*, reemphasized the evident similarities of the genera and noted that Myers, in a personal communication, questioned the distinctiveness of the nominal genera.

Recent collecting activities in the Corantijn River system of western Surinam yielded a third species of characiform with a protractile mouth. The new species, *Bivibranchia bimaculata*, inhabits the main river channels, rocky pools, and creeks in the black water systems of that basin. Studies associated with the description of the species led to a reevaluation of the distinctiveness of *Bivibranchia* and *Atomaster*. These anatomical investigations revealed a series of additional synapomorphies for the species of *Bivibranchia* (sensu lato).

*Methods and materials.*—Counts of total vertebrae were taken from radiographs and cleared and stained specimens, and include the four vertebrae of the Weberian apparatus, with the fused  $PU_1 + U_1$  of the caudal skeleton counted as a single element. Numbers in parentheses after a vertebral count are the number of specimens with that particular count. In counts of the pelvic and median rays, unbranched rays are indicated by Roman numerals and branched rays by Arabic numerals. The ranges for meristic counts are based on the holotype and paratypes, with the value for the holotype indicated in square brackets.

Specimens examined for this study are deposited in the following institutions: American Museum of Natural History, AMNH; Academy of Natural Sciences of Philadelphia, ANSP; British Museum (Natural History), BMNH; National Museum of Natural History, Smithsonian Institution, USNM. Specimens cleared and counterstained for cartilage and bone are indicated by CS.

In his discussion of the Bivibranchiinae, Roberts (1974:432) noted that *Atomaster* Eigenmann and Myers (1927) was originally distinguished from *Bivibranchia* Eigenmann (1912) by differences in scale form and number, but that the taxa were, at least externally, otherwise very similar, and that Myers (personal communication) now questioned the necessity for the recognition of separate genera. Roberts was, however, unable to pursue further the question of generic distinctiveness in the absence of comparative material of the single species of *Atomaster* (*A. velox*). Examination of a cleared and counterstained specimen of *Atomaster* shows that the genus shares the distinctive morphological modifications noted by Eigenmann (1912:258–259) and Roberts (1974:432–433) for *Bivibranchia*. These characters include the valvular processes on the roof of the mouth, the unusual fleshy ridges on the surfaces of the epibranchials and ceratobranchials, the pronounced restructurings of the upper jaw and suspensorium which permit pronounced protractility of the upper jaw, and the numerous distinctive adaptations of gill arch osteology described by Roberts for *Bivibranchia protractila*. Those shared derived characters along with the unique synapomorphies described below unite *Bivibranchia protractila*, *Atomaster velox*, and *Bivibranchia bimaculata*, described in this paper, as a phylogenetically monophyletic, and morphologically very distinctive subunit of the family Hemiodontidae. In light of those numerous derived similarities and given the few differences in scale form and number that are the primary distinguishing characters of the nominal genera, I follow Myers' suggestion and formally place *Atomaster* Eigenmann and Myers as a synonym of *Bivibranchia* Eigenmann. *Bivibranchia* in that more inclusive sense is used throughout the remainder of the paper.

Apomorphic modifications of two previously unanalyzed body systems serve further to characterize *Bivibranchia* and provide additional evidence that the three contained species (*protractila*, *velox*, *bimaculata*) constitute a monophyletic lineage within the Hemiodontidae. The first set of these synapomorphies involves the association of the anteriormost pleural ribs with the vertebral column, and the system of ligamentous connections of these ribs to each other. In all other hemiodontids and most characiform outgroups examined, the parapophyses associated with the anterior full pleural ribs are approximately round elements, each of which inserts into a circular or ovoid articular fossa limited to the lateral surface of its respective centrum (see Weitzman 1962:fig. 12). *Bivibranchia* alternatively has a marked vertical expansion of the articular fossae and parapophyses asso-



ciated with the third and fourth full pleural ribs. This restructuring results in distinctly dorsoventrally elongate parapophyses and a parallel vertical lengthening of the associated articular fossae. Correlated with the restructuring of the parapophyses is the dorsal expansion of the portions of the third and fourth pleural ribs proximate to the vertebral column. A relatively slender bone rounded in cross section is the typical and hypothesized primitive condition of the proximate portion of the shaft of the pleural rib in characiforms. In *Bivibranchia* this section of the rib is apomorphously expanded dorsally into a transversely aligned, vertically triangular plate. This elaboration of the parapophyses, articular fossae, and ribs is similar to that described by Vari (1983:41–42, fig. 37) for the genera *Caenotropus* and *Chilodus* of the Chilodontidae. Differences in the identity of the ribs and vertebrae involved in this complex in *Bivibranchia* on the one hand, and chilodontids on the other raise questions as to the homology of the characters in the involved taxa. In chilodontids the first through third full pleural ribs all show the described modifications, with distinctly greater vertical development of the articular fossa, parapophysis, and proximal portion of the shaft of the rib on the second full pleural rib. In *Bivibranchia*, in contrast, the first two ribs, their articular fossae and associated parapophyses are unelaborated. Differences in the fourth pleural rib and the associated parapophyses and articular fossae also distinguish the two taxa. Chilodontids retain the conditions of those elements generalized for characiforms, whereas in *Bivibranchia* the proximal portions of the fourth pleural rib and the associated articular fossae and parapophyses are expanded dorsally to a degree equivalent to that on the third pleural rib.

The hypothesis of the homoplasy of these modifications in *Bivibranchia* and the Chilodontidae is, furthermore, congruent (parsimoniously consistent) with available phylogenetic information about the groups. Outgroup comparisons within the Hemiodontidae have not revealed any comparable pleural rib and vertebral alterations in *Argonectes*, the taxon most closely related to *Bivibranchia* (Roberts 1974), nor in any of the other examined genera in the family (*Anodus*, *Hemiodopsis*, *Hemiodus*, *Micromischodus*). The absence of pleural rib alterations in close relatives of *Bivibranchia* in conjunction with the closer phylogenetic association of the Chilodontidae with the Anostomidae, Curimatidae, and Prochilodontidae (Vari 1983:46–47) makes it most parsimonious to hypothesize that these similarities in *Bivibranchia* on the one hand, and the Chilodontidae on the other, represent convergencies at the level of the two involved taxa rather than synapomorphies for a lineage consisting of the Chilodontidae and *Bivibranchia*.

The second derived pleural rib associated modification shared by the three species of *Bivibranchia* is the presence of well developed intercostal ligaments interconnecting the four anteriormost full pleural ribs. A thick posterodorsally slanting ligamentous band arises from the posterior surface of the first full pleural rib, extends past, but does not contact the medial surface of the second rib, and attaches to the anterior margin of the dorsal portion of the third rib. A second thick intercostal ligament arises from the posterior surface of the first pleural rib ventral of the insertion of the first ligament, extends past the medial surfaces of the second and third ribs, again without direct contact, and attaches to the anterior surface of the fourth pleural rib. Somewhat similar versions of such intercostal connections are present in the other hemiodontid genera examined (*Argonectes*, *Hemiodopsis*, *Hemiodus*, *Micromischodus*), but in those taxa the intercostal con-

nections are thin, flattened, strap-like bands rather than the thick cord-like structures characteristic of *Bivibranchia*. Thus the intercostal bands in those hemiodontid outgroups are more similar to the broad, thin connective tissue sheet that joins the pleural ribs along their medial surfaces in most characiforms. As such the connections in hemiodontids other than *Bivibranchia* may represent an intermediate step in a transition series that resulted in the evolution of the system of well developed intercostal ligaments in that genus. A complex of intercostal ligaments somewhat comparable to those in *Bivibranchia* was described by Vari (1983:41–42, fig. 36) in the Anostomidae and Chilodontidae, with a system of thick ligaments in the Chilodontidae most comparable to the pleural rib interconnections of *Bivibranchia*. The intercostal ligament complex in chilodontids differs, however, from that in *Bivibranchia* in having a dorsal ligamentous attachment of the first and second ribs not found in *Bivibranchia*, and in the absence of the ligament attaching the first and fourth ribs that is present in that genus. Furthermore the intercostal ligament in chilodontids that spans the first to third ribs is attached to the medial surface of the second rib, whereas in *Bivibranchia* the ligaments and the medial surfaces of the intervening ribs are distinctly separated by an intermediate tissue layer. These morphological differences raise questions as to the homology of the intercostal connections in the two groups, *Bivibranchia* and the Chilodontidae. Such a hypothesis of the non-homology of the modifications in the two taxa is congruent with the available data on phylogenetic relationships noted above which indicate that *Bivibranchia* and the Chilodontidae are not each other's closest relatives.

The functional basis for the expansion of the intercostal ligaments and the vertical elongation of the articular fossae, parapophyses, and ribs in *Bivibranchia* is obscure, but may be correlated with the head-down feeding orientation of members of the genus (personal observations on *B. bimaculata*). This feeding position parallels the more pronounced head-down swimming orientation typical of members of the Chilodontidae which homoplasiously demonstrate comparable morphological adaptations.

The second set of synapomorphies for the species of *Bivibranchia* is the series of hypertrophied modifications of the portion of the nervous system associated with the branchial basket. Most noteworthy is the hypertrophy of the nerve complex serving the gill arches, and the associated elaboration of the vagal lobes of the medulla oblongata. Among the numerous restructurings of the *Bivibranchia* branchial basket noted by Roberts (1974:420–421), one of the more conspicuous is the pronounced vertical expansion of the epibranchials and ceratobranchials via thin bony lamina. The surfaces of these expanded gill arch elements are covered by specialized layers of epithelial tissue with “. . . a uniform series of prominent finely papillose ridges.” Each ridge is associated with a gill raker, and the ridges on opposing surfaces of the gill arches interdigitate when in contact. The vertical expansion of the epibranchials and ceratobranchials in addition to markedly increasing the surface area of the gill arches, also accommodates a change in the form of the central channel of the epibranchials and ceratobranchials of the first three gill arches. On these ossifications, the shallow median groove on the abpharyngeal surface of the bone that is typical of characiforms is expanded into a deep central trough. These troughs serve at least in part for the support of a greatly expanded nerve network innervating the anterior portion of the gill arches. Two



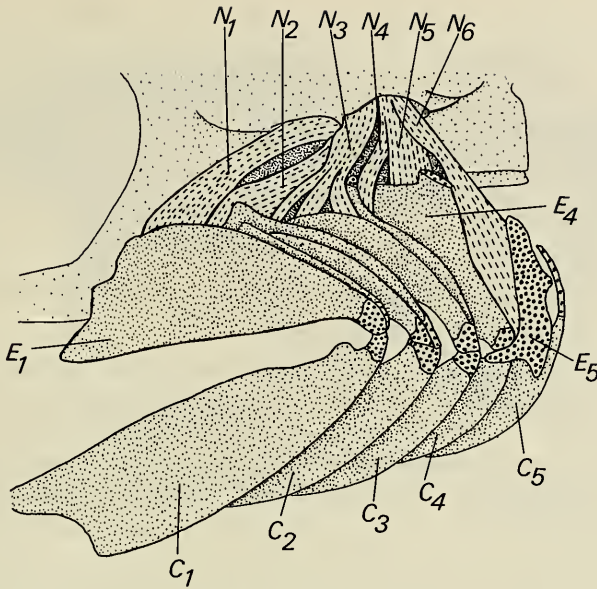


Fig. 1. *Bivibranchia bimaculata*, USNM 268203, paratype, gill arches, glossopharyngeal and vagus nerves, and posteroventral portion of neurocranium, left side, lateral view. Abbreviations: C—ceratobranchials (1 to 5); E—epibranchials (1 to 5, 2 and 3 not labelled); N—branches of hypertrophied nerve complex ( $N_1$ —glossopharyngeal nerve,  $N_2$  to  $N_6$ —vagus nerve). Large stippling indicates cartilage, dashed lines indicate nerves.

primary trunks of cranial nerves form this hypertrophied nerve complex. In lateral view (Fig. 1) this complex is seen as a diverging series of large nerves that exit the neurocranium dorsal of the gill arches and pass ventrally into the branchial basket. The nerve complex passes through the wall of the neurocranium via two proximate enlarged foramina on the anteroventral surface of the exoccipital. These expanded apertures are visible as the enlarged openings in the exoccipitals as illustrated by Roberts (1974:fig. 24) in the ventral view of the skull of *Bivibranchia*. The enlargement of these foramina is particularly obvious when they are compared to the homologous openings in *Hemiodus* and *Argonectes* (Figs. 4 and 21 of Roberts).

The smaller anterior exoccipital foramen is the point of exit for the anteriormost nerve bundle (Fig. 1,  $N_1$ ) which is part of the ninth cranial (glossopharyngeal) nerve. After exiting the skull, that nerve trunk extends ventrally into the medial margin of the central trough of the first epibranchial, diverges laterally in that element, with a smaller portion of the nerve continuing into the first ceratobranchial through the epibranchial-ceratobranchial joint. The remaining five major branches of the nerve complex innervating the gill arches all exit from the larger foramen located immediately posterior of the foramen for the glossopharyngeal nerve (Fig. 1,  $N_2$  to  $N_6$ ), and are all components of the tenth cranial (vagus) nerve. The anteriormost of these ( $N_2$ ) has two subunits. The anterior branch of  $N_2$  extends to the posterior surface and ventral margin of the first epibranchial, and the larger posterior section of  $N_2$  enters the medial portions of the central trough of the second epibranchial within which it has a distribution comparable to the primary

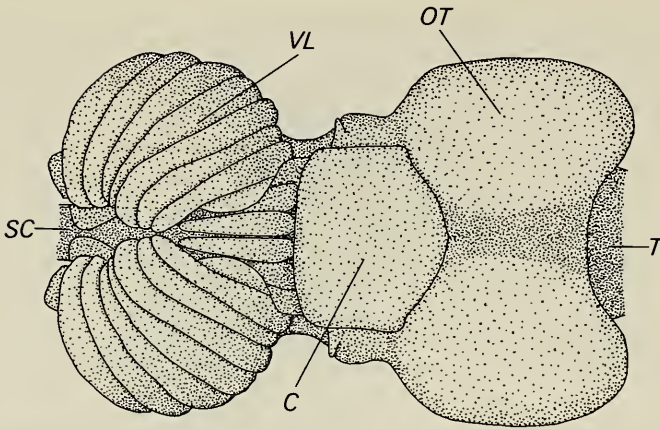


Fig. 2. *Bivibranchia protractila*, USNM 225491, brain, posterior portion, dorsal view, anterior to right. Abbreviations: C—cerebellum; OT—optic tectum; SC—spinal cord; T—telencephalon; VL—vagal lobe of medulla oblongata.

nerve branch in the first epibranchial, and with a section continuing into the second ceratobranchial. The next major nerve bundle ( $N_3$ ) has three subsections. The anteriormost branch runs to the posterior surface and ventral margin of the second epibranchial, and the two remaining portions of  $N_3$  enter the central trough of the third epibranchial, and are distributed in that element and the third ceratobranchial in a pattern comparable to that noted for the primary nerves of the first and second gill arches. The fourth nerve ramus ( $N_4$ ) innervates the posterior surface of the third epibranchial, and the fifth major nerve branch ( $N_5$ ) runs along the posterior portion of the fourth epibranchial with relatively few grossly obvious branches before continuing onto the dorsal surface of the fourth ceratobranchial. The sixth and final section of the complex ( $N_6$ ) extends over the lateral surface of the fourth epibranchial before passing medial to the enlarged cartilaginous fifth epibranchial to innervate the anterior and dorsal surfaces of the fifth ceratobranchial.

The very large nerve bundles innervating the gill arches in *Bivibranchia* represent a hypertrophy of the glossopharyngeal (IX) and vagus (X) nerve complex relative to the much narrower nerves typical of other characiforms and most teleostean fishes (e.g., *Menidia*, Bernstein 1970:fig. 18). Information from other groups of fishes indicates that the ninth and tenth cranial nerves consist of both visceral sensory and visceral motor components. It is not possible to determine at present whether the dramatic increase in the size of these nerves in the species of *Bivibranchia* represents the hypertrophy of only one of these components, or whether both components of those nerves are involved. The question of the degree to which the increased size of the nerves is correlated with an increased degree of proprioception of the gill arch elements, chemoreception for analysis of potential food items in the pharyngeal cavity, some combination of the above, or perhaps another function is similarly unresolved.

Not unexpectedly the dramatic enlargement of the glossopharyngeal (IX) and vagus (X) nerves is reflected in grossly obvious modifications of the central nervous

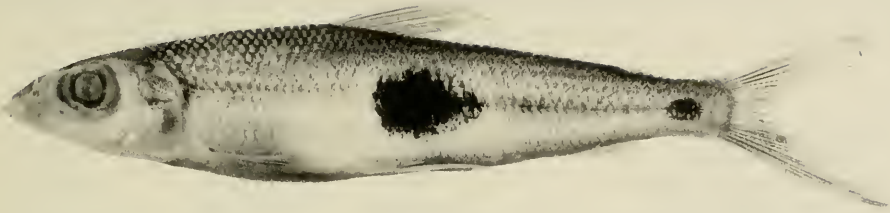


Fig. 3. *Bivibranchia bimaculata*, new species, holotype, USNM 225974, 80.5 mm SL.

system. Moderately developed vagal lobes of the medulla oblongata occur in various ostariophysans (Bernstein 1970:55, fig. 3) and within the Hemiodontidae have been found in both *Hemiodus* and *Hemiodopsis*. In *Bivibranchia* both of the enlarged cranial nerves (IX and X) communicate with the central nervous system at the base of the vagal lobe of the medulla oblongata, and the enlargement of the vagal lobes of the medulla oblongata is carried even further. The vagal lobes in *Bivibranchia* (Fig. 2) are dramatically enlarged into bulbous structures that are distinctly expanded laterally and extend to the level of the dorsal surface of the cerebellum. More striking is the elaboration of the surface of the markedly enlarged vagal lobes of the medulla oblongata into a series of posterodorsally oriented folds which cover the anterior, dorsal, and lateral surfaces of the lobes. These derived elaborations of this portion of the central nervous system are not apparent in other hemiodontids or other characiforms examined and are consequently considered synapomorphies for the three species of *Bivibranchia*. The functional significance of these vagal lobe elaborations is unknown, although they are presumably correlated with the hypertrophy of the associated glossopharyngeal and vagus nerves.

*Bivibranchia bimaculata*, new species

Fig. 3, Table 1

*Holotype*.—USNM 225974, 80.5 mm standard length (SL), collected by R. P. Vari and L. R. Parenti, 17 Sep 1980, in a rocky pool in the center of the Corantijn River at "Camp Hydro," Nickerie District, Surinam (approx. 3°42'N, 57°58'W).

*Paratypes*.—All from Nickerie District, Surinam: 12 specimens taken with holotype: ANSP 153656, 1 specimen, 94.5 mm SL; BMNH 1984.10.23:1, 1 specimen, 97.8 mm SL; AMNH 55611, 1 specimen, 86.7 mm SL; USNM 268203, 9 specimens, 68.3–94.7 mm SL (1 specimen CS). 1 specimen, BMNH 1981.6.8:816, 68.2 mm SL, collected by H. M. Madarie, 18 May 1980, in a small creek draining from the right bank of the Corantijn River near Mataway (approx. 4°58.5'N, 57°42'W). 7 specimens, AMNH 54807, Dalbana Creek, 150 m upstream of junction with the Kabalebo River (approx. 4°47'N, 57°26'W).

*Non-type specimens examined*.—All from Nickerie District, Surinam: 7 specimens, USNM 225491, same data as BMNH 1981.6.9:816 (1 specimen CS). 49 specimens, USNM 268204, taken with holotype, juveniles (3 specimens CS). 5 specimens, AMNH 54817, small stream entering Kabalebo River, 150 m upstream of mouth of Dalbana Creek. 1 specimen, AMNH 54835, stream draining



Table 1.—Morphometrics of *Bivibranchia bimaculata*, new species. Standard length is expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 15 proportions of head length.

	Holotype	Paratypes (20)	
		Range	Average
Standard length	80.5	68.2–97.8	82.69
1. Greatest body depth	0.24	0.22–0.26	0.243
2. Snout to dorsal-fin origin	0.49	0.47–0.51	0.489
3. Snout to anal-fin origin	0.81	0.80–0.84	0.820
4. Snout to pelvic-fin origin	0.56	0.54–0.58	0.561
5. Snout to anus	0.79	0.79–0.82	0.802
6. Origin of rayed dorsal fin to hypural joint	0.53	0.51–0.56	0.544
7. Least depth of caudal peduncle	0.09	0.09–0.10	0.093
8. Pectoral-fin length	0.20	0.19–0.22	0.200
9. Pelvic-fin length	0.19	0.18–0.20	0.189
10. Head length	0.28	0.27–0.30	0.285
11. Snout length	0.34	0.30–0.34	0.313
12. Orbital diameter	0.38	0.34–0.38	0.358
13. Postorbital head length	0.34	0.32–0.36	0.351
14. Interorbital width	0.37	0.34–0.39	0.357
15. Gape width	0.13	0.11–0.13	0.124

into Kabalebo River near Camp Avanavero, about 5 km downstream of DeVis Falls. 14 specimens, AMNH 54858, side channel of Kabalebo River, 1 km south of Avanavero Falls. 13 specimens, AMNH 54926, same locality as holotype. 13 specimens, AMNH 54959, rocky side pool of Corantijn River approximately 378 km from its mouth. 1 specimen, BMNH 1981.6.9:839, stream at km 212 of Amotopo-Camp Geology road, at "Machine Park." 1 specimen, USNM 225195, small stream entering Lucie River, 3 km upstream of junction of Lucie and Kabalebo rivers.

*Diagnosis.*—*Bivibranchia bimaculata* shares with the two other species of the genus a number of modifications of the jaws, branchial apparatus, anterior ribs, vertebral column, glossopharyngeal and vagus nerves, and vagal lobe of the medulla oblongata that distinguish the genus within the Hemiodontidae (see discussion above). The presence in *Bivibranchia bimaculata* of a large spot of dark pigmentation on the midlateral body surface centered slightly posterior of the vertical through the insertion of the posteriormost dorsal fin ray, and of a small darkly pigmented midlateral spot on the caudal peduncle separates the species from *B. protractila* and *B. velox* which have plain bodies. The 49 to 55 pored lateral line scales to the hypural joint, 8½ or 9½ scales in a transverse series above the lateral line to the origin of the dorsal fin, and the possession of cycloid scales distinguish *B. bimaculata* from *B. velox* which has 80 or more series of scales to the hypural joint, 12 to 16 scales in a transverse series to the origin of the dorsal fin, and ctenoid scales. The longer pelvic fins (0.18–0.20 of SL), 8 branched anal-fin rays, and typically 11, sometimes 10, branched pelvic-fin rays of *B. bimaculata* further separate that species from *B. protractila* in which the pelvic fins are 0.14–0.17 of SL, and which has 7 branched anal-fin rays, and 9, rarely 10, pelvic-fin rays.



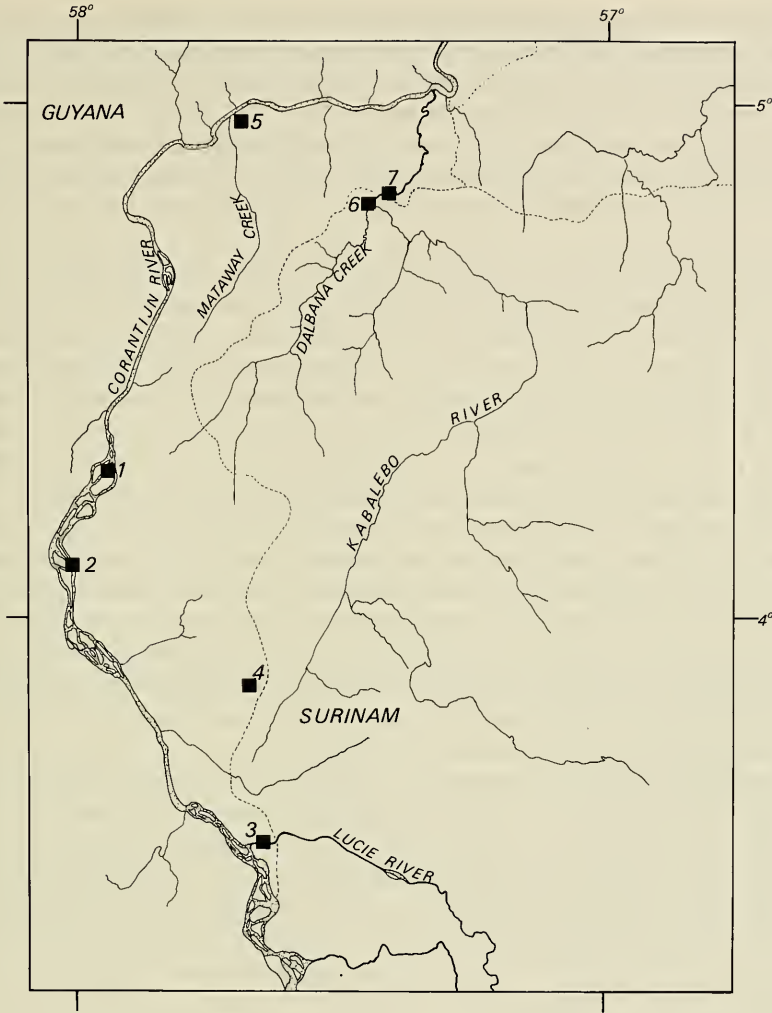


Fig. 4. Map of the middle portion of the Corantijn River basin region, Surinam and Guyana, showing collecting localities of specimens reported on in this paper (dotted lines depict road systems in area): 1, “Camp Hydro,” type locality; 2, Km 378 of Corantijn River; 3, Lucie River; 4, “Machine Park”; 5, creek near Mataway; 6, Dalbana Creek; 7, Camp Avanavero and Avanavero Falls. Some squares indicate more than one locality or more than one lot of specimens. See listing of holotype, paratypes, and non-type specimens examined for detailed locality and collection information.

*Description.* — Morphometrics of the holotype and paratypes are given in Table 1. Body slender, slightly compressed laterally. Greatest body depth at origin of rayed dorsal fin. Dorsal profile of body gently curved from tip of snout to caudal peduncle. A slight median keel immediately anterior of origin of dorsal fin. Ventral profile of body smoothly convex from tip of lower jaw to caudal peduncle. Ventral surface of body transversely flattened anteriorly.

Head pointed in profile, interorbital region flattened. Fronto-parietal fontanel extensive, extending into rear of ethmoid and onto dorsal portion of supraoccip-

ital. Parietals completely separated, frontals in contact only at epiphyseal bar. Upper jaw longer than lower jaw, highly protractile. Nostrils approximate, anterior opening round, posterior crescent shaped, partially closed by flap of skin separating nostrils. Eye relatively large. A large, horizontally ovoid "adipose eyelid" (a thick transparent connective tissue layer) extends from under nostrils posteriorly to opercle, thicker anteriorly; thicker and more developed longitudinally in larger specimens. Adipose eyelid with an ovoid, vertically elongate opening overlying pupil.

Lower jaw edentulous, rounded in ventral view, anterior margin fleshy. Upper jaw with a single series of functional teeth. All teeth tricuspidate, 7 on each side of jaw in all cleared and stained specimens examined (30–82 mm SL); teeth becoming progressively larger medially. A single row of partially formed replacement teeth internal to functional tooth row. Replacement tooth row embedded in flesh of inner surface of upper jaw. Dermopalatine and ectopterygoid edentulous. Fifth ceratobranchial bearing a relatively narrow band of posterodorsally directed teeth along medial and posteromedial borders; teeth along anterior portion of band elongate, tricuspidate; those along posterior margin elongate, conical. Fourth and fifth upper pharyngeal tooth-plates with a band of elongate tricuspidate teeth. Gill rakers elongate, with short side processes. Gill rakers extend along surfaces of vertically expanded ceratobranchials and epibranchials. Surfaces of expanded ceratobranchials and epibranchials with series of fleshy ridges aligned nearly perpendicular to their primary axes. Gill arches highly modified, innervated by hypertrophied glossopharyngeal and vagus nerves (see description above). Gill membranes narrowly attached medially to urohyal.

Scales cycloid, firm. Pored lateral line scales between supracleithrum and hypural joint 49 to 55 [55]. Five to 8 pored lateral line scales extending beyond hypural joint onto base of caudal fin. Scales above lateral line in a transverse series to origin of rayed dorsal fin  $8\frac{1}{2}$  or  $9\frac{1}{2}$  [ $9\frac{1}{2}$ ]. Scales below lateral line in a transverse series to origin of anal fin 5 or 6 [6]. Body squamation extending onto base of caudal fin rays. Axillary process of pelvic fin formed by a single enlarged scale.

Vertebrae 38 (20), 39 (3).

Rayed dorsal fin obtusely pointed, second unbranched and first branched rays longest, subequal. Dorsal-fin rays ii,9 or iii,9 [iii,9]; when three unbranched rays present, first very short. Adipose dorsal fin of moderate size, unscaled. Anal fin obtusely pointed, anterior branched rays over twice length of posteriormost rays. Anal-fin rays ii,8 or iii,8 [ii,8]; when three unbranched anal-fin rays present, first very short. Pectoral fin pointed, reaching two-thirds of distance to vertical through origin of pelvic fin. Dorsalmost rays of pectoral fin correspond to a distinct groove along side of body formed by a connective tissue ridge extending posteriorly from posterior margin of cleithrum. Pelvic fin pointed, reaching slightly over one-half distance to anus. Pelvic-fin rays i,10 or i,11 (typically i,11) [i,11].

*Coloration in life.*—Overall coloration silvery with a greenish grey shading; silvery coloration more intense on ventral portions of body. Dark midlateral spot on body very obvious; spot on caudal peduncle somewhat masked.

*Coloration in preservative.*—Overall coloration in specimens fixed in formalin and preserved in ethanol light tan. Head darker on dorsal portions, particularly in interorbital region and across parietals. A broad band of scattered chromatophores extends over dorsal half of opercle. Overall coloration of body darker



dorsally. A deep-lying dusky band along lateral line, pigmentation of band more intense posteriorly. A distinct dark, round or horizontally ovoid spot with irregular margins on midlateral surface of body. Spot extends 8 to 13 scales horizontally and 4 to 7 scales dorsally. Spot centered along or slightly posterior of vertical through insertion of last dorsal-fin ray, and somewhat dorsal of lateral line. A smaller darkly pigmented, round or horizontally ovoid spot on caudal peduncle immediately anterior of hypural joint. Caudal peduncle spot faint in larger individuals, absent in some large specimens. Caudal and rayed dorsal fins dusky, with fin-rays outlined by series of chromatophores. Adipose dorsal fin hyaline.

Juveniles with scale margins outlined by series of chromatophores. Midlateral body spot absent in specimens under 20 mm SL. Midlateral caudal peduncle spot not developed in smaller individuals.

*Etymology.*—The specific name, *bimaculata*, from the Latin *bi*, two, and *macula*, spot, refers to the two dark spots on the lateral surface of the body and caudal peduncle.

*Ecology.*—*Bivibranchia bimaculata* is widely distributed throughout the acid, black waters of the Corantijn River system of western Surinam above the region of tidal influence. It is most common in areas of sandy beaches and in rocky pools, with juveniles often also found in smaller side streams, sometimes a considerable distance from the main river channels. This species has been observed travelling in large schools over sandy beaches, evidently feeding on food items which individuals separate out of the substrate by manipulation of mouthfulls of sand.

*Comparative material examined.*—*Bivibranchia protractila* Eigenmann: GUY-ANA: BMNH 1972.10.17:1378–1397, 15 specimens, Rupununi River; USNM 197104, 13 specimens, Rupununi River; BMNH 1936.4.4:17–18, 2 specimens, Rockstone; BMNH 1911.10.31:484, 2 specimens, Rockstone, paratypes of *B. protractila*; USNM 66126, 1 specimen, Rockstone, paratype of *B. protractila*; BMNH 1934.9.12:291, 1 specimen, Mazaruni River; BMNH 1972.7.27:81–109, 27 specimens, Rupununi District, Jacaré; USNM 268205, 5 specimens, Essequibo River (2 specimens CS). BRAZIL, Mato Grosso: USNM 194302, 1 specimen, Rio Juruena; USNM 194287, 2 specimens, Rio Juruena.

*Bivibranchia velox* Eigenmann and Myers: USNM 268345, 1 specimen, Brazil, Pará, Rio Tocantins (CS).

*Argonectes longipinnis* Steindachner: USNM 243224, 2 specimens, Brazil, Roraima, Rio Jauaperi (1 specimen CS).

*Anodus elongatus* Spix: USNM 231550, 1 specimen, Peru, Loreto, Río Ucayali (CS).

*Hemiodopsis ocellata* Vari, USNM 225593, 1 specimen, Surinam, Nickerie District, Corantijn River (CS).

*Hemiodus* species, USNM 231551, 2 specimens, Brazil, Mato Grosso, Rio Arinos (CS).

*Micromichodus sugillatus* Roberts, USNM 205527, 1 specimen, Brazil, Pará (CS).

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Department of Vertebrate Zoology (Fishes), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.